JHR 93: 71–80 (2022)
doi: 10.3897/jhr.93.90545
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

A new fossil euphorine genus and species (Hymenoptera, Braconidae) with the longest known ovipositor from Dominican amber

Sergey A. Belokobylskij[1], Tomáš Hovorka[2,3]

1 *Zoological Institute of the Russian Academy of Sciences, St Petersburg 199034, Russia* **2** *Department of Entomology, National Museum, Cirkusová 1740, Prague 19300, Czech Republic* **3** *Department of Zoology, Charles University, Viničná 1594, Prague 12800, Czech Republic*

Corresponding author: Tomáš Hovorka (hovorkarl@gmail.com)

Academic editor: Jose Fernandez-Triana | Received 10 August 2022 | Accepted 3 October 2022 | Published 31 October 2022

https://zoobank.org/20468409-9032-48A8-948F-3EFD0EF2C5C9

Citation: Belokobylskij SA, Hovorka T (2022) A new fossil euphorine genus and species (Hymenoptera, Braconidae) with the longest known ovipositor from Dominican amber. Journal of Hymenoptera Research 93: 71–80. https://doi.org/10.3897/jhr.93.90545

Abstract

A new genus and species of the braconid subfamily Euphorinae, *Palaeorionis longicaudis* **gen. et sp. nov.**, is described and illustrated from Miocene Dominican amber. This new genus is characterised by the long and tube-shaped petiole, presence of both radiomedial (2-SR and r-m) veins on the infuscate fore wing and long ovipositor.

Keywords

Aridelus, description, fossil, Miocene, *Orionis*, ovipositor, petiole, *Stenothremma*

Copyright *S.A. Belokobylskij & T. Hovorka.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The subfamily Euphorinae is one of the most diverse groups of koinobiont parasitoids of the family Braconidae, which are known to attack larval, nymphal, and adult stages of hosts from the insect orders Orthoptera, Hemiptera, Psocoptera, Raphidioptera, Neuroptera, Coleoptera, Lepidoptera and Hymenoptera (Tobias 1965, 1966; Shaw 1985; Yu et al. 2016).

Most of the known fossil euphorine taxa have been described from amber (Brues 1933, 1937, 1939; Tobias 1987), though a few of its representatives are known from compression fossils (Belokobylskij 2014). Aside from the relatively common fossil parasitoids of coleopteran and lepidopteran larvae from the genus *Meteorus* Haliday, 1835 of the tribe Meteorini, parasitoids of hemipteran nymphs and coleopteran and hymenopteran adults have been also discovered. There are species of the genus *Leiophron* Nees, 1819 (*Euphorus* Nees, 1834) (Euphorini) parasitods of the hemipteran nymphs, the genera *Pygostolus* Haliday, 1833 (Pygostolini), *Parasyrrhizus* Brues, 1933 (Centistini), *Microctonus* Wesmael, 1835, and perhaps *Onychoura* Brues, 1933 and *Meteorites* Brues, 1939 (Perilitini) (Brues 1933, 1937, 1939) are known to parasitize coleopteran and hymenopteran hosts. The extinct genus *Elasmosomites* Brues, 1933 actually belongs to the isolated euphorine tribe Neoneurini, whose members are parasitoids of the ant workers (Brues 1933; Belokobylskij et al. 2021). Additionally, two peculiar genera that are only known from the Baltic amber have unknown biologies, namely *Oncometeorus* Tobias, 1987 from the monotypic tribe Oncometeorini and *Prosyntretus* Tobias, 1987 from the Prosyntretini (Tobias 1987).

This study provides an illustrated description of the female of a new euphorine genus and species from the Miocene Dominican amber that is characterised by the long tube-shape petiolate first metasomal tergite and long ovipositor.

Methods

Dominican amber (Lower Miocene age; 20–15 Ma) is the fossilized resin of the leguminose tree *Hymenaea protera* Poinar, being mostly transparent and often containing a high number of fossil inclusions, and it has been collected in various sites within the Dominican Republic (Iturralde and Macphee 1996; Rasnitsyn and Quicke 2002).

During the present study, fossil braconid specimen were examined using a Leica M205 C stereomicroscope (Microsystems, Wetzlar, Germany). Photographs were obtained using a Keyence VHX-5000 (Mechelen, Belgium) digital microscope under suitable magnifications. Subsequent image processing was performed using Helicon Focus Pro 7 software. Final plates were prepared in Adobe Photoshop CS6.

The terminology employed for morphological features, sculpture and body measurements follows Belokobylskij and Maeto (2009). Wing venation nomenclature also follows Belokobylskij and Maeto (2009), with the terminology of van Achterberg (1993) shown in parentheses.

The material used for this study is deposited in the collection of the Stuttgart Museum of Natural History, Germany (**SMNS**).

Results

Systematic part

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1811
Subfamily Euphorinae Foerster, 1863

Genus *Palaeorionis* gen. nov.
https://zoobank.org/3DBBCBF8-D9A1-455C-857A-F76B18E09778
Figs 1, 2

Type species. *Palaeorionis longicaudis* gen. et sp. nov., by present designation and monotypy.

Etymology. Named after "palaeo" (Greek for "ancient") and the generic name of its similar extant genus, *Orionis*, which belongs to the subfamily Euphorinae. Gender: masculine.

Description. ***Head*** (Fig. 1B, C) weakly transverse. Ocelli rather large and distinctly convex. Frons weakly convex. Eyes large, elongate-oval, glabrous. Face distinctly convex. Malar space very short; malar suture perhaps absent. Clypeus complete, distinctly convex (lateral view); hypoclypeal depression absent. Occipital carina distinct laterally, perhaps widely interrupted dorsally (Fig. 1B). Mandibles relatively small. Maxillary palpus very long (Fig. 1C), perhaps 6-segmented (medial segments hidden by mesosoma), its apical segment very long and slender, almost 25.0 times longer than its maximum width. Labial palpus short, with 4 segments, third segment very small, tiny, subglobular; apical (fourth) segment longest, knife-shaped, narrowed towards apex.

Antenna (Fig. 1A, C) long, slender, filiform, about 33-segmented. Scapus rather short and wide. Pedicel relatively small. First flagellar segment subcylindrical, without any transformations, much longer than its apical width, about as long as second segment. Apical segment pointed apically, but without spine.

Mesosoma (Fig. 1C, D, E). Sides of pronotum rugose upper and areolate below. Mesoscutum perhaps smooth, narrowly reticulate laterally. Notauli present, perhaps almost complete and shallow especially posteriorly. Scutellum distinctly convex. Prepectal carina present, sharp and distinct. Mesopleuron mainly smooth. Precoxal sulcus present, long, not deep, curved, distinctly crenulate-reticulate. Metascutum without dorsal tooth (lateral view). Propodeum dorsally almost straight in basal two-thirds, distinctly oblique sloped, starting from basal third, without lateral tubercles (in lateral view).

Wings (Fig. 1G). Fore wing rather narrow, pterostigma long and rather narrow. Radial (marginal) cell weakly shortened, narrow, about 4.5 times longer than its maximum width. Metacarpus (1-R1) 1.2 times longer than pterostigma. First medial abscissa (1-SR+M) present and curved. Present both radiomedial veins (2-SR and r-m). Second radiomedial (submarginal) cell short, pentagonal. Discoidal (first discal) cell not petiolate anteriorly, sessile. Recurrent vein (m-cu) postfurcal, subparallel to basal vein (1-M). First

mediocubital vein (M+CU1) well sclerotised and distinctly sinuate. Nervulus (cu-a) postfurcal. Brachial (first subdiscal) cell open posteriorly; brachial vein (CU1b) absent. Transverse anal veins (1a and 2a) absent. Hind wing. Submedial (subbasal) cell short. First abscissa of mediocubital vein (M+CU) distinctly shorter than second abscissa (1-M).

Figure 1. *Palaeorionis longicaudis* gen. et sp. nov. (holotype, female) **A** habitus, lateral view **B** head, latero-posterior view **C** head, antenna and mesosoma, lateral view **D** mesosoma without propodeum, lateral view **E** propodeum, lateral view **F** hind coxa **G** wings.

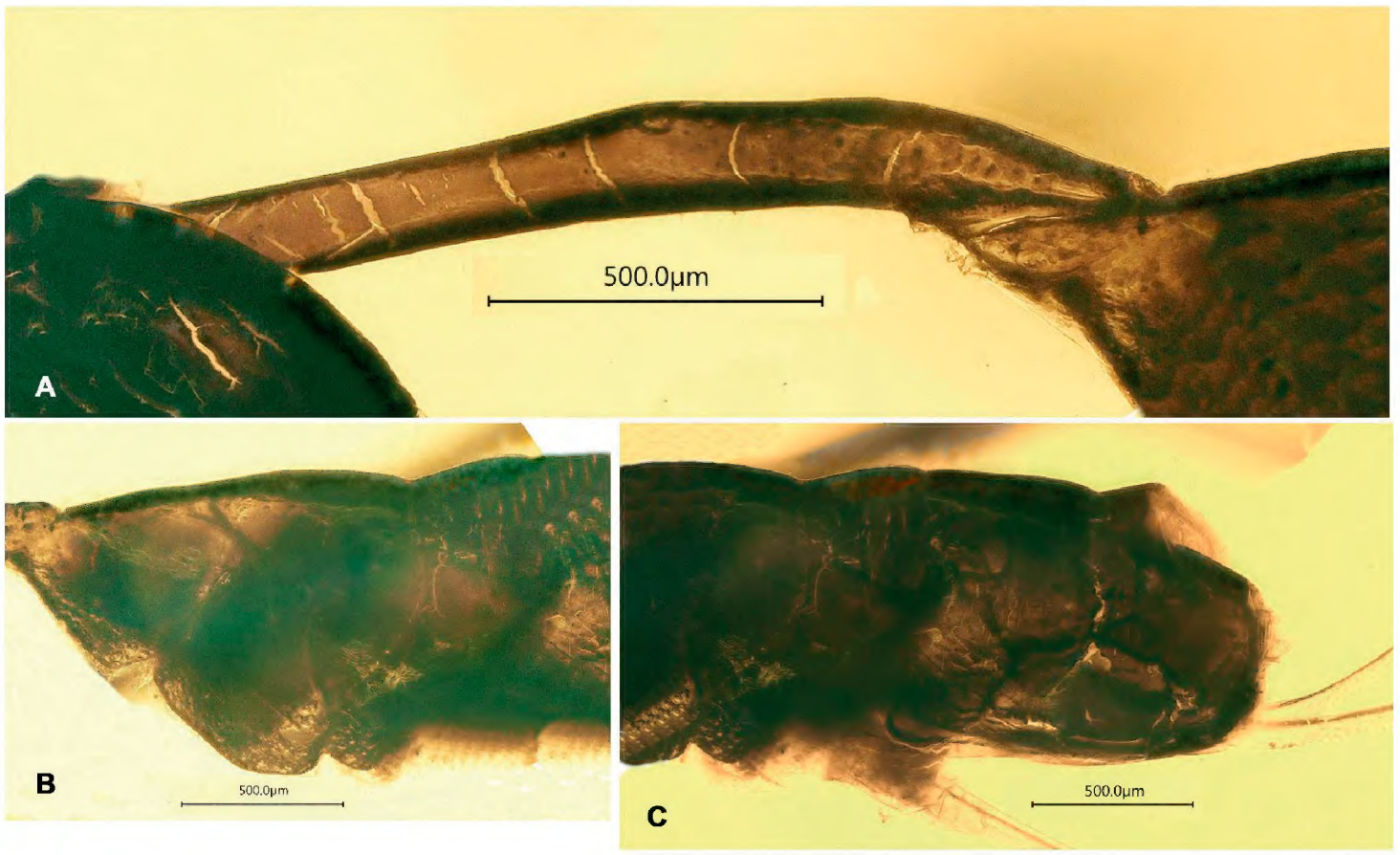

Figure 2. *Palaeorionis longicaudis* gen. et sp. nov. (holotype, female) **A** petiole, lateral view **B** anterior half of metasoma without petiole (gaster), lateral view **C** posterior half of metasoma, lateral view.

Legs (Fig. 1A, F) slender and very long. Hind coxa elongate, without ventro-basal tubercle, as long as propodeum. Hind femur long and slender, 0.8 times as long as hind tibia. Hind tibia narrow basally, distinctly widened in apical 0.8. Hind tibial spurs relatively short, 0.3 times as long as hind basitarsus. Hind basitarsus about 0.8 times as long as second-fifth segments combined. Tarsal claw small and simple.

Metasoma (Figs 1A, 2) elongate, compressed behind petiole, entirely smooth, segments behind third one distinctly exposed posteriorly. First metasomal tergite very narrow entirely, fused ventrally almost entirely, tubular, smooth dorsally, with spiracles situated behind middle of petiole, without dorsope and laterope; 0.6 times as long as mesosoma and metasoma behind petiole. Suture between second and third tergites absent. Laterotergites (epipleura) of all segments not separated. Ovipositor long, weakly curved, compressed basally. Ovipositor sheath 1.2 times longer than the body length, almost twice longer than mesosoma, 1.1 times longer than fore wing (Fig. 1A).

Comparative diagnosis. *Palaeorionis* gen nov. is characterised by a long and tube-like petiole resembling a similar structure in some extant Euphorinae genera, especially *Aridelus* Marshall, 1887, *Chrysopophthorus* Goidanich, 1948, *Orionis* Shaw, 1987, *Stenothremma* Shaw, 1984, and *Wesmaelia* Foerster, 1863.

Palaeorionis gen. nov. differs from *Orionis* Shaw by having the last segment of the maxillary palpus very long and narrow (shorter and thicker in *Orionis*), discoidal (discal) cell of infuscate fore wing sessile (petiolate in hyaline fore wing in *Orionis*), second radiomedial vein (r-m) present (absent in *Orionis*), mediocubital vein (M+CU1) sinuate (straight in *Orionis*), brachial (subdiscal) cell long and rather narrow (short and

wide in *Orionis*), petiole of metasoma smooth and without any carinae (at least partly sculptured and with lateral carinae in *Orionis*), and ovipositor sheath longer than metasoma (distinctly shorter in *Orionis*).

Palaeorionis gen nov. differs from *Aridelus* Marshall by having the last segment of maxillary palpus very long and narrow (shorter and thicker in *Aridelus*), mesosoma relatively long (short in *Aridelus*), hind coxa distinctly elongate-oval (shortly oval in *Aridelus*), mesosoma without areolate sculpture (entirely areolate in *Aridelus*), mediocubital vein (M+CU1) of fore wing sinuate (straight in *Aridelus*), hind femur relatively wide (narrow in *Aridelus*), metasoma rather compressed and with distinctly exposed apical segments (not compressed and retracted apical segments as in *Aridelus*), and ovipositor sheath longer than metasoma (very short and usually concealed inside of the metasoma in *Aridelus*).

The newly described genus also differs from *Stenothremma* Shaw by the last segment of the maxillary palpus very long and narrow (shorter and thicker in *Stenothremma*), mesosoma relatively long (short in *Stenothremma*), hind coxa distinctly elongate-oval (subglobal in *Stenothremma*), body without granulate sculpture (head, mesosoma and petiole densely granulate in *Stenothremma*), discoidal (discal) cell of infuscate fore wing sessile (petiolate in hyaline fore wing in *Stenothremma*), second radiomedial vein (r-m) present (often absent in *Stenothremma*), mediocubital vein (M+CU1) sinuate (straight in *Stenothremma*), brachial (subdiscal) cell long and rather narrow (short and wide in *Stenothremma*), petiole of metasoma smooth (petiole mainly granulate in *Stenothremma*), and ovipositor sheath longer than metasoma (distinctly shorter in *Stenothremma*).

The differences from the extant genera *Wesmaelia* and *Orionis* are summarized in Table 1.

Table 1. The differences between the Palaeorionis gen nov. and two similar recent genera (*Wesmaelia* Foerster and *Chrysopophthorus* Goidanich).

Genus Character	***Palaeorionis* gen. nov.**	***Wesmaelia***	***Chrysopophthorus***
1. Last segment of the maxillary palpus	very long and narrow	shorter and thicker	shorter and thicker
2. Pedicel of antenna	distinctly enlarged, more than half as long as scape	short, much less than half of the length of scape	distinctly enlarged, about half as long as scape
3. Mesosoma	relatively long	short	short
4. Colour of fore wing	infuscate	hyaline	hyaline
5. Second radiomedial vein (r-m) of fore wing	present	absent	present
6. Mediocubital vein (M+CU1) of fore wing	sinuate	straight	straight
7. Discoidal (discal) cell of fore wing	sessile	petiolate	petiolate
8. Hind coxa	distinctly elongate-oval	weakly oval	weakly oval
9. Hind femur	widened	narrow	narrow
10. Metasoma	rather compressed and with distinctly exposed apical segments	not compressed and with retracted apical segments	not compressed and with retracted apical segments
11. Ovipositor sheath	longer than metasoma	very short and usually concealed inside of metasoma	distinctly shorter than metasoma

Between the known fossil Euphorinae genera, *Palaeorionis* gen nov. is similar to *Onychoura* Brues, 1933 (with type species *O. petiolata* Brues, 1933) and *Meteorites* Brues, 1939 (with type species *M. inopinata* Brues, 1939), both from Baltic amber. This new genus differs from *Onychoura* by having malar area short (very long in *Onychoura*), mesosoma relatively elongated (very short in *Onychoura*), notauli present (perhaps absent in *Onychoura*), propodeum long (very short in *Onychoura*), radial (marginal) cell of fore wing weakly shortened (strongly shortened in *Onychoura*), recurrent vein (m-cu) distinctly postfurcal (interstitial in *Onychoura*), petiole of metasoma not swollen (swollen in *Onychoura*), and ovipositor longer than metasoma and without apical hook (distinctly shorter and with very slender apical hook in *Onychoura*). *Palaeorionis* gen nov. distinctly differs from *Meteorites* Brues by the last segment of maxillary palpus very long and narrow (much shorter and thicker in *Meteorites*), antenna long, about 33-segmented (short, 13–14-segmented in *Meteorites*), mesosoma relatively long, about twice longer than height (short, about as long as height in *Meteorites*), second radiomedial vein (r-m) of fore wing present (absent in *Meteorites*), nervulus (cu-a) and recurrent (m-cu) veins distinctly postfurcal (almost interstitial in *Meteorites*), petiole of metasoma not widened distally and almost straight (widened distally and distinct evenly curved in *Meteorites*), and ovipositor longer than metasoma and almost straight (distinctly shorter and strongly arcuate in *Meteorites*).

***Palaeorionis longicaudis* sp. nov.**

https://zoobank.org/42C8A588-A16D-4E8E-A1FC-8C304CE98D78

Figs 1, 2

Type material. ***Holotype*:** Female, preserved in Lower Miocene Dominican amber (20–15 Ma), deposited in SMNS under collection number Do-2886-D. Well preserved, complete parasitoid inside amber piece (50 × 40 × 20 mm).

Description. Female. Body length 7.7 mm; fore wing length 4.6 mm.

***Head*:** Head not depressed, relatively high. Occiput at least weakly concave. Temple rather short. Transverse diameter of eye 3.7 times longer than temple (lateral view). Eye large, about 1.5 times as high as broad (lateral view). Malar suture perhaps absent. Malar space short. Clypeus without lower flange. Mandible rather short. Fourth segment of labial palpi the longest, 4.5 times longer than its maximum width, 1.7 times longer than second segment.

***Antenna*:** First flagellar segment subcylindrical, 6.2 times longer than its apical width, as long as second segment; second segment 5.5 times longer than its apical with. Submedial segments about 2.5 times longer than their width. Penultimate segments short, 1.2–1.3 times longer than its width, 0.4 times as long as apical segment.

***Mesosoma*:** Mesosoma relatively long, not depressed, its length about 2.0 times height. Neck of prothorax short. Mesoscutum highly and convex-roundly elevated above pronotum, its median lobe convex, weakly protruding forward, perhaps without anterolateral corners. Prescutellar depression (scutellar sulcus) invisible. Subalar depression shallow and sculptured. Mesopleuron widely smooth; metapleuron rugose.

***Wings*:** Fore wing narrow, 3.9 times longer than its maximum width. Pterostigma about 5.0 times longer than width. Radial vein (r) arising behind middle of pterostigma, from basal 0.6. First (r) and second (3RSa) radial abscissae forming very obtuse angle. Second radial abscissa (3RSa) almost equal to first abscissa (r), 0.1 times as long as the straight third abscissa (3RSb), 0.2 times as long as the almost straight first radiomedial vein (2RS). Second radiomedial (submarginal) cell relatively narrow and short, 1.6 times longer than its maximum width, 0.6 times as long as the wide brachial (first subdiscal) cell. Brachial (first subdiscal) cell almost straight anteriorly. First medial abscissa ((RS+M) a) slightly curved. Recurrent vein (1m-cu) almost 0.5 times as long as first radiomedial vein (2RS), 0.3 times as long as basal vein (1M). Discoidal (first discal) cell rather long, 3.2 times longer than its maximum width. Nervulus (1cu-a) postfurcal, almost 2.0 times longer than distance from basal (1M) vein and nervulus (1cu-a). Parallel vein (2CUb) arising from posterior 0.2 of apical margin of brachial (second subdiscal) cell. Brachial (second subdiscal) cell long and wide. Hind wing relatively narrow. Radial (marginal) cell weakly widened basally and narrowed apically, without additional transverse vein (r). Nervellus (cu-a) present, oblique. Submedial (subbasal) cell short. First abscissa of mediocubital vein (M+CU) 0.6 times as long as second abscissa (M).

***Legs*:** Fore trochanter almost twice longer than trochantellus. Fore tarsus almost as long as fore tibia. Hind coxa 2.0 times longer than maximum width, 0.7 times as long as petiole. Hind femur 6.5 times longer than width. Hind tarsus slender, 0.8 times as long as hind tibia. Second segment of hind tarsus 0.5 times as long as basitarsus, almost 2.0 times longer than fifth segment (without pretarsus).

***Metasoma*:** Metasoma 1.2 times longer than head and mesosoma combined. First metasomal tergite 9.6 times longer than medial high (at spiracles level), tergite ventrally fused in basal 0.8. Lateral suture between second and third tergites present, but dorsal suture absent. Second and third tergites combined 0.7 times as long as following tergites. Hypopygium short, obtuse distally, strongly retracted below under metasoma, almost glabrous.

***Sculpture*:** Vertex and temple mainly smooth. Hind coxa and femur smooth. Metasoma entirely smooth. Hind tibia with rather dense and short semi-erect setae, its length 0.2–0.3 times maximum width of tibia.

***Colour*:** Body almost entirely black or dark brown. Antenna mainly light brown. Labial palpi light brown; maxillary palpi dark reddish brown, but at least apical segment brownish yellow. Legs mainly dark brown, all tibiae basally yellow at short distance. Ovipositor sheaths light brown, infuscate apically. Fore wing almost entirely distinctly infuscate, paler basally and apically, with distinct hyaline transverse stripe under base of pterostigma. Pterostigma mainly dark brown, pale brown in basal fifth.

Male. Unknown.

Etymology. Named from Latin "longus" (= long) and "caudus" (= tail, ovipositor) because this taxon has the longest known ovipositor of all fossil Euphorinae taxa.

Discussion

The fossil braconid taxa from the subfamily Euphorinae are relatively common in the Paleogene in comparison to the members of some other braconid subfamilies. They were often attributed as representatives of extant genera, however various of these fossil taxa actually belong to peculiar extinct taxa, namely *Elasmosomites* Brues, *Meteorites* Brues, *Oncometeorus* Tobias, *Onychoura* Brues, *Parasyrrhizus* Brues and *Prosyntretus* Tobias (Brues 1933, 1937, 1939; Tobias 1987, Belokobylskij 2014, Belokobylskij et al. 2021). These euphorine genera were recorded from the inclusions found in the Baltic and Canadian ambers (Brues 1933, 1939, 1937; Tobias 1987) and were placed in the tribes Meteorini, Oncometeorini, Perilitini, Centistini, Euphorini, Prosyntretini and Neoneurini.

The tubular petiole of the mesosoma is practically unknown from previously recorded fossil euphorine taxa. In this situation, the genus *Palaeorionis* gen nov., is the first extinct genus having such long tube-shaped petiole. Perhaps only *Onychoura* Brues, 1933 from Baltic amber possessed a petiole with similar structure, but it is much shorter and thickened towards the apex. The new genus is also well characterised by the distinctly infuscate fore wing having submedially only a single narrow transverse subhyaline stripe, very long ovipositor (much longer than metasoma), and distinctly thickened tibia of the hind leg. This character combination is unknown in all previously recorded amber euphorine genera.

The host of *Palaeorionis longicaudis* gen. et sp. nov. is unclear. However, based on available characters such as a long ovipositor and presence of both radiomedial veins (2-SR and r-m) in the fore wing this genus likely belongs to the tribe Meteorini, whose members are known to be endoparasitoids of coleopteran and lepidopteran larvae. Regarding its long ovipositor, this species might have been a parasitoid of some concealed hosts such as wood-boring beetles.

Acknowledgements

Authors are thankful to Stuttgart Museum of Natural History (Germany) for the loan of the amber piece. We are also thankful to Dr Julia Stigenberg (Stockholm, Sweden), Prof Donald J. Quicke for their useful consultations, Dr Petr Janšta and Jonah Ulmer for their useful tips and final corrections.

The authors are very thankful to Dr Alejandro Zaldívar-Riverón (UNAM, México) and Prof Cornelis van Achterberg (Naturalis, Leiden, The Netherlands) for their very useful comments on the first version of the manuscript.

This study was supported by The Charles University Grant Agency (GAUK), project No. 375421 (TH) and performed as a part of the State Research Project No 122031100272-3 (SAB).

References

Belokobylskij SA (2014) Family Braconidae. In: Antropov AV, Belokobylskij SA, Compton SG, Dlussky GM, Khalaim AI, Kolyada VA, Kozlov MA, Perfilieva KS, Rasnitsyn AP (Eds) The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the insect limestone (Late Eocene) of the Isle of Wight, UK. Earth and Environmental Sciences Transactions of the Royal Society of Edinburgh 104 (3–4): 335–446. https://doi.org/10.1017/S1755691014000103

Belokobylskij SA, Dubovikoff DA, Manukyan AR, Zharkov DM (2021) Braconid parasitoids of ants (Hymenoptera, Braconidae, Euphorinae, Neoneurini) from Baltic amber with a discussion of records of fossil larvae parasitizing ant workers. Journal of Hymenoptera Research 84: 29–43. https://doi.org/10.3897/jhr.84.67749

Belokobylskij SA, Maeto K (2009) Doryctinae (Hymenoptera, Braconidae) of Japan. Fauna mundi, Vol. 1, Warszawa, Warshawska Drukarnia Naukowa, 806 pp. https://doi.org/10.3161/067.058.0107

Brues CT (1933) The parasitic Hymenoptera of the Baltic amber. Bernstein Forschungen 3: 4–178.

Brues CT (1937) Superfamilies Ichneumonoidea, Serphoidea, and Chalcidoidea. In: Carpenter FM, Folsom JW, Essig EO, Kinsey AC, Brues CT, Boesel MW, Ewig HE (Eds) Insects and arachnids from Canadian amber. University of Toronto Studies. Geological Series 40: 27–44.

Brues CT (1939) New Oligocene Braconidae and Bethylidae from Baltic amber. Annals of the Entomological Society of America 32: 251–263. https://doi.org/10.1093/aesa/32.2.251

Iturralde MA, Macphee RDE (1996) Age and paleogeographical origin of Dominican amber. Science 273: 1850–1852. https://doi.org/10.1126/science.273.5283.1850

Rasnitsyn AP, Quicke DLJ (2002) History of insects. Kluwer Academic Publishers, New York, Boston, Dordrecht, London, Moscow, 517 pp. https://doi.org/10.1007/0-306-47577-4

Shaw SR (1985) A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). Entomography 3: 277–370.

Tobias VI (1965) Generic grouping and evolution of parasitic Hymenoptera of the subfamily Euphorinae (Hymenoptera, Braconidae). I. Entomologicheskoe Obozrenie 44: 841–865. [In Russian]

Tobias VI (1966) Generic grouping and evolution of parasitic Hymenoptera of the subfamily Euphorinae (Hymenoptera, Braconidae). II. Entomologicheskoe Obozrenie 45: 612–33. [In Russian]

Tobias VI (1987) New taxa of Braconidae from Baltic amber (Hymenoptera). Entomologicheskoe Obozrenie 66(4): 845–859. [English translation: Entomological Review 67(4): 18–32.] [In Russian]

van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 283.

Yu DS, van Achterberg C, Horstmann K (2016) Taxapad 2016. Ichneumonoidea 2015. Nepean, Ottawa, Ontario. [database on flash-drive]